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NOTES ON THE ECOLOGY OF *AZORELLA SELAGO* HOOK. f.

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ABSTRACT

The umbelliferous cushion plant *Azorella selago* Hook f. is one of the most important constituents of Subantarctic plant communities. The species was studied during a fifteen months survey of the vegetation of Marion Island, South Indian Ocean. Aspects reported on include the species distribution on the Island, rôle in the vegetation, vitality, growth form, leaf production, annual height increase, age of cushions and primary aerial production.

UITTREKSEL

NOTAS OOR DIE EKOLOGIE VAN *AZORELLA SELAGO* HOOK. f.

Die polplant *Azorella selago* Hook f. (Umbelliferae) is een van die belangrikste bestandele van subantartiese plantgemeenskappe. Die spesies was gedurende 'n vyftien maand lange ondersoek na die plantegroei van Marion Eiland (in die Suidelike Indiese Oseaan) bestudeer. Aspekte waaroor verslag gedoen is sluit in die verspreiding van die spesies oor die Eiland, rol in die plantegroei, lewenskrag, groei vorm, blaar produksie, jaarlikse hoogte toename, ouderdom van pol en primêre bogrondse produksie.

INTRODUCTION

Azorella selago Hook. f. is one of the most prolific and ubiquitous vascular plants of the subantarctic islands. It plays an important and conspicuous rôle in the vegetation of the Marion and Prince Edward Islands, Iles Crozet, Archipel de Kerguelen, Macquarie and Heard Island, being absent from only South Georgia in the Subantarctic zone. Its remarkable growth form (Figures 1 and 2) immediately attracts the attention of visitors to the islands, not only as an outstanding example of adaptation to the harsh environment, but also as a welcome cushion for the weary explorer of these rugged, tractless islands.

During an extensive survey of the vegetation of Marion Island (Huntley, 1968, 1971) it was possible to investigate some aspects of this interesting plant's ecology. Neither time nor facilities were available for sophisticated autecological studies; it is hoped however that the preliminary findings presented here will stimulate a detailed study of this most interesting plant.

STUDY AREA

Marion Island (46°55′S, 37°45′E) is an extremely isolated volcanic island lying in the South Indian Ocean. The Island experiences an isothermal oceanic

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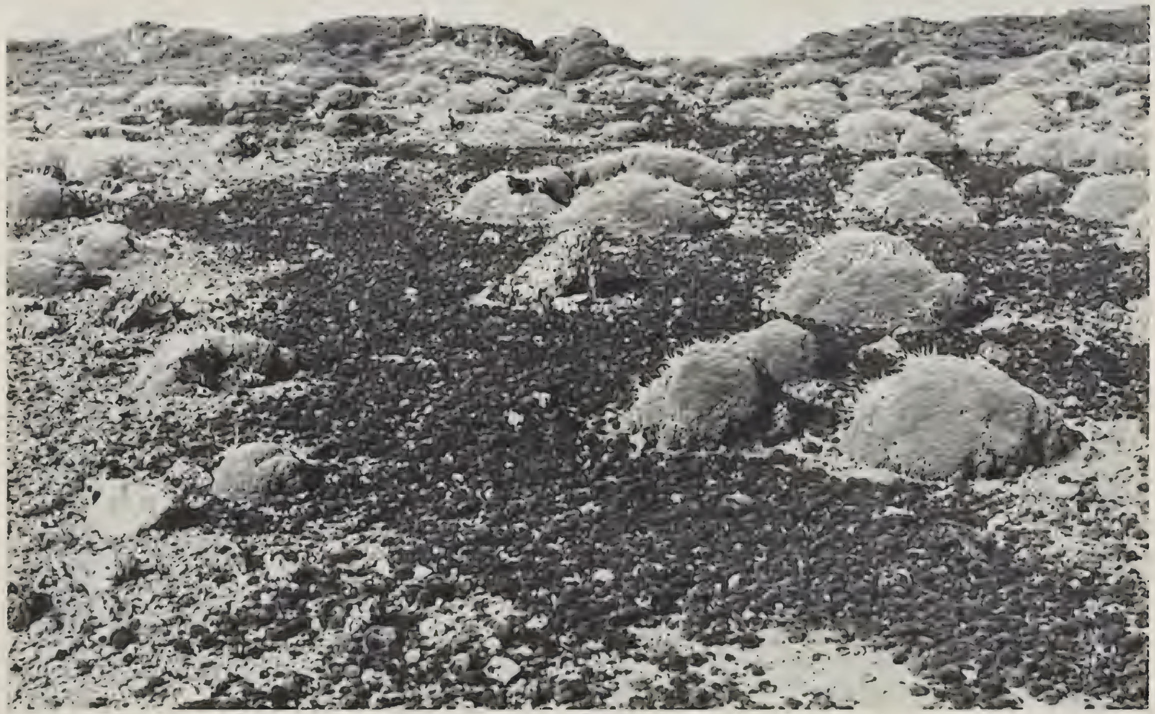

Fig. 1.

Azorella selago growing in a fjaeldmark community on an exposed ridge on Prince Edward Island. Tufts of the grass *Agrostis magellanica* grow 'epiphytically' on the *Azorella selago* cushions while numerous balls of the mosses *Andreaea regularis* and *Ditrichum strictum* occupy the loose lava between the cushions.

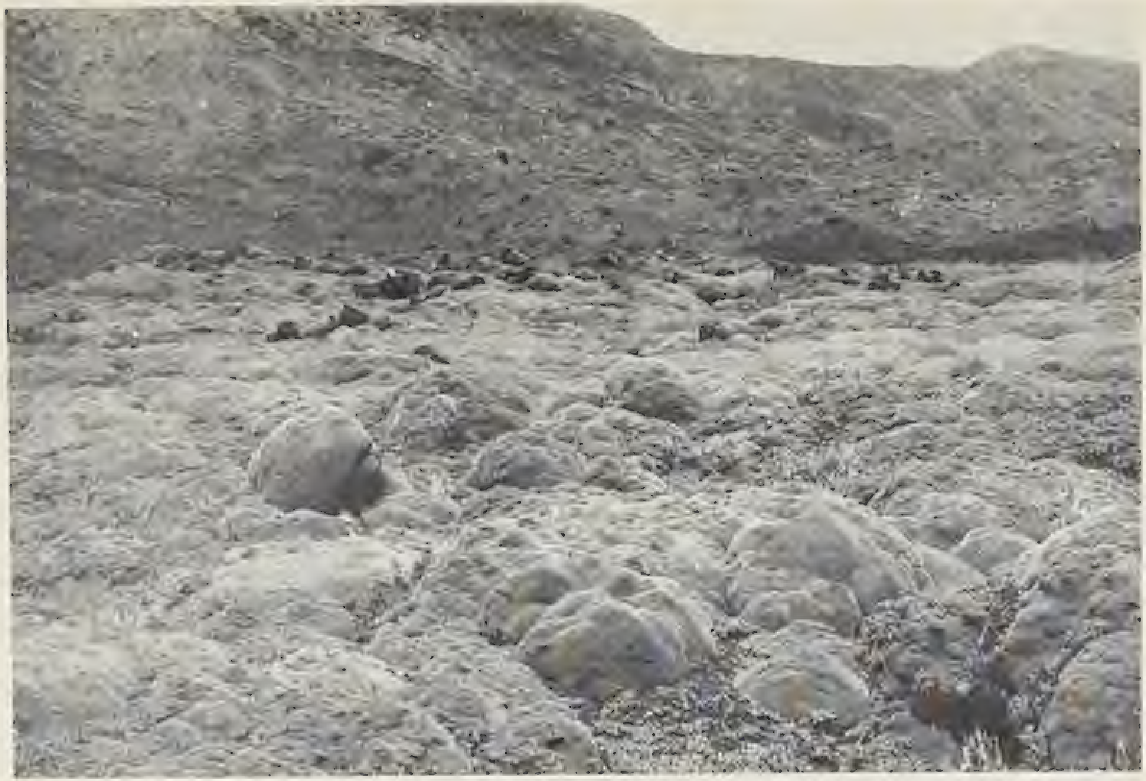

FIG. 2.
Exceptionally large spongy cushions of *Azorella selago* forming an almost continuous carpet over black lava on the west coast plain of Marion Island.

tundra climate, with a mean temperature of 5,5°C (range of mean monthly temps: 3,6 to 7,8°C). Precipitation is recorded on over 300 days per annum, the total averaging 2 576 mm. The Island is approximately 300 square kilometers in area with the topography rising steeply from the cliff-lined coast to the highest peaks at slightly above 1 200 m.

In common with other subantarctic islands, no trees are found on Marion Island, the vegetation comprising short, closed herbaceous communities on the lowlands and open cryptogamic communities at altitudes above 500 m.

STUDY METHODS

As opportunities presented themselves, various aspects of the biology of *Azorella selago* were studied. While most of these studies formed part of the extensive ecological survey certain aspects such as growth rate, growth form, vitality, etc., were given special attention. Populations rather than individuals were studied and as a rule at least twenty plants from each population were sampled where quantitative measurements were taken.

Distribution of Azorella selago on Marion Island

Over 1 500 km were covered on foot during the survey of the Island. Thus a comprehensive idea of *A. selago's* distribution was obtained.

Rôle of Azorella selago in the Islands vegetation

A quantitative and qualitative study of the plant communities was made using a quadrat technique (Huntley 1967, 1968, 1971) in which 457 stands of the various communities were examined. In each quadrat the cover, sociability and vitality of plants were recorded in addition to habitat factors.

Vitality

The vitality of *Azorella selago* was recorded qualitatively following the Zoller (1954) scale, according to which 1 = strongly reduced, sick or very weak; 2 = clearly reduced vitality, but still healthy; 3 = normal and 4 = very strong and vigorous. A quantitative measure of the vitality of *A. selago* populations growing in several habitats was obtained by measuring the length and breadth of leaves taken at random from a large sample.

Growth form

Typical examples of the various cushion forms exhibited by *A. selago* were examined in profiile and scale drawings made of aerial and subterranean organs.

Leaf production

A. selago leaves turn brown in autumn and it is thus easy to distinguish the new green leaves produced the following spring. It was therefore possible to count the number of new leaves produced per shoot through the growth period. Populations of *A. selago* in seven habitats were examined at fortnightly intervals during the 1965–66 season.

Annual height increase and age of cushions

Slender stakes of 30 to 50 cm in length were inserted into cushions and secured in the soil substrate, care being taken not to damage branches or roots. The stakes were marked at the upper end by two lines 1 cm apart, the lower of these being brought opposite the smooth convex surface of the cushion. The stakes were placed in position in May 1965 and the height increase measured in late March 1966 and early April 1969. Height increase was determined by measuring the distance between the new cushion surface and the upper line, and subtracting from 1 cm.

Primary aerial production

Normal harvest methods could not be applied to measure the primary aerial production of *A. selago*. This is due to the plant's compact cushion growth form which makes clipping of an even sample of the season's growth impossible, and secondly to the very low cover and scattered pattern of cushions which would require an impractically large number of samples for any measure of accuracy. Instead of sampling a community as a whole, individual cushions were removed *in toto* in April 1970 and the leaf production of the 1969–70 season was estimated by removing and weighing samples of shoots produced during that season. Only three cushions were avalable for study, one from herbfield and two from fjaeldmark. The mean number of shoots per 100 sq. cm were counted in triplicate and the mean dry weight of samples of 200 heads determined. An estimate of the net primary production for the individual cushions, and for the communities in which they occurred could then be calculated.

RESULTS AND DISCUSSION

Distribution of Azorella selagoon Marion Island. A. selago proved to be the most ubiquitous vascular plant on the Island, occuring from sea level to the extreme limit of vascular plant growth at 765 m, (Huntley 1970). With the exception of sites permanently submerged in over 20 cm of water, it may be said that *A. selago* occurred in every habitat in which vascular plants were recorded.

Rôle of A. selago in the vegetation. The importance of *A. selago* in the vegetation may be gauged by the fact that it occurred in 71 % of the 457 quadrats (10 × 10 m) examined in the vegetation survey, followed by *Agrostis magellanica* (65 %), *Poa cookii* (57 %) and *Ranunculus biternatus* (47 %) in order of frequency. *A. selago* was present in all twelve of the "noda" recognised in the vascular vegetation (Huntley 1968, 1971) and was the dominant species in three of these.

Besides its rôle as the dominant plant in many communities, it is also a pioneer of many areas, stabilizing recent lava flows and scoreaceous slopes and providing a substrate for colonization by less hardy species such as *Ranunculus biternatus, Montia fontana, Callitriche antarctia, Colobanthus kerguelensis, Agrostis magellanica, Poa cookii, Uncinia dikei* and many other species which grow 'epiphytically' on the cushions.

Vitality. A. selago is certainly the most robust plant on the Island, with the widest ecological amplitude. Table 1 presents a summary of the observed vitality of *A. selago* populations growing in the main habitat types available to vascular plant growth on the Island.

TABLE 1

Vitality of *Azorella selago* populations occupying various habitats on Marion Island, according to the scale of Zoller (1954).

Habitat conditions	Vitality	Plant community
well drained eutrophic soils	4	Azorella selago herbfield
sites protected from wind	4	Azorella selago herbfield
sites exposed to strong wind	3	Azorella selago fjaeldmark
sites exposed to heavy salt spray . . .	2	Tillaea moschata halophytic herbfield
sites occupied by birds and seals . . .	2	Poa cookii tussock grassland
waterlogged oligotrophic soil	2	Agrostis magellanica mire
sites temporarily or permanently submerged	1	Tarn hydrosere

Growth form. One of the most interesting features of *A. selago* is its cushion-like growth form which is perhaps surprising in a member of the carrot family. This form is not unique to Azorella however; as early as 1912 Hauri described 337 cushion forming flowering plants, from 34 families. The possible advantages of this growth form are discussed by Huntley (1968, 1971).

The growth form of *A. selago* is most typically a hard compact cushion of 15 30 cm height and 20 40 cm diameter. Such cushions are extremely resistant to damage or injury by frost or wind action. Reiche (1907) remarks that a cushion of *Azorella madreporica* of Chile turned off a revolver bullet!

The shape of individual cushions varies considerably. In *Azorella-Poa* Montane Herbfield for example, the cushions spread out forming a continuous carpet over several score square metres, while in *Azorella selago* Herbfield on the Island's west coast plain, enormous cushions in excess of 1 m height are found. These cushions are extremely spongy and offer no resistance to compression.

In plan the cushions are rarely circular except in very young plants. Most cushions in exposed sites develop an arcuate shape, advancing into the wind. The rate of advance appears to be extremely slow, cushions marked in February 1965 had advanced less than two centimetres by April 1969. Nevertheless the position of the plants is definitely not static, as witnessed in cushions that had advanced several decimeters over pipelines, posts and other structures erected fifteen to twenty years ago.

In profile, the cushions exhibit a great diversity of form. In optimum habitats the cushions are large and spongy, contrasting with the small compact cushions

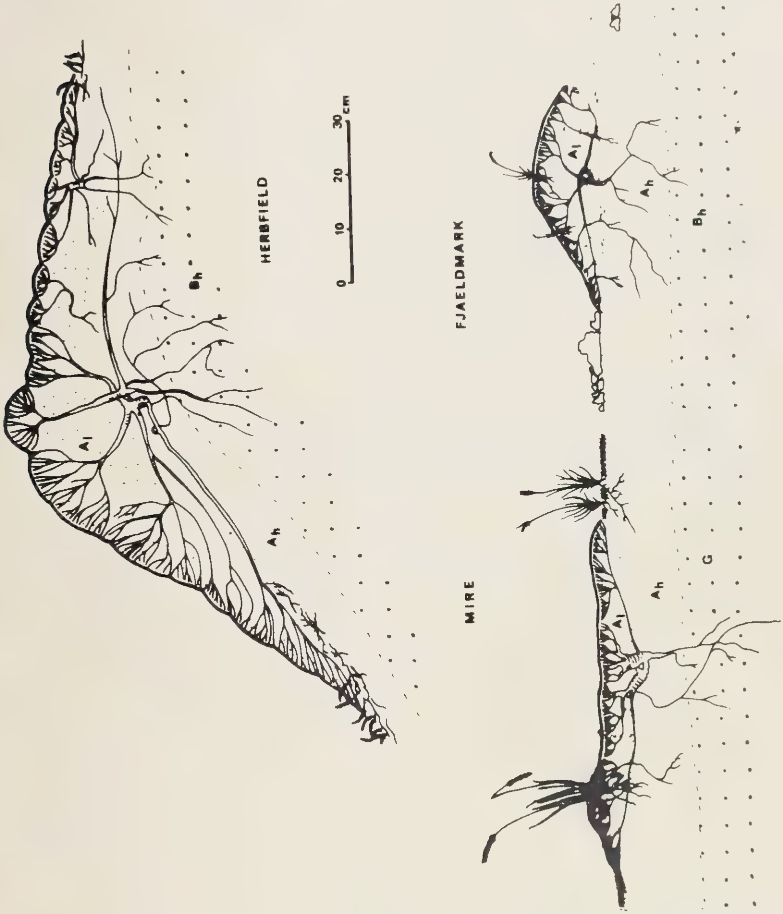

Fig. 3.
Profile diagrams of typical cushions of *Azorella selago* examined in various habitats.

of windswept fjaeldmark. In swampy sites the cushions never attain more than a few centimeters in height, usually spreading out as a rough mat (Figure 3).

Leaf production. During 1965 *Azorella selago* cushions on Marion Island ceased vegetative growth in mid-April and by mid-June the cushions were dark brown. Early in July a few new green leaf buds were noted in cushions of lowland and well protected upland populations and by the end of August all plants examined had at least one new leaf (Figure 4).

In the optimum habitat studied, well drained eutrophic soils in a sheltered valley at 140 m a.s.l., an average of nine new leaves per shoot had opened fully by mid February 1966 compared with six in an exposed herbfield community on well-drained eutrophic soils, five in ill drained oligotrophic mire and five in very exposed fjaeldmark.

By mid-March 1966 the full complement of new leaves had appeared, and towards the end of March most leaves showed signs of autumnal colouring. With the possible exception of *Poa cookii* and *Poa annua*, *Azorella selago* appears to have the longest growth season of Marion Island vascular plants, ranging from seven and a half months in exposed upland sites to eight and a half months in protected habitats.

Annual height increase of cushions. The height increases recorded in five populations during the period May 1965 to April 1969 are presented in Table 2. The mean annual height increase in the fjaeldmark populations was only 1,8 mm, while that of the most robust population growing in optimum habitat conditions was only 6,0 mm per annum. This latter figure compares with that of $\frac{1}{4}$ inch (6,35 mm) given by Taylor (1955) for *A. selago* on Macquarie Island. Taylor (*op. cit.*) does not state in which habitat the measurement was made however; it is possible that in exposed fjaeldmark communities the growth may be much less than the figure he gives.

TABLE 2
Height increase in *Azorella selago* cushions during the period 1965–69.

site	plant community (Huntley, 1968)	altitude, m	exposure to wind	height increase, mm		
				1965–66	1965–69	mean annual
1	Azorella selago fjaeldmark	150	exposed plain	2,4	7,3	1,8
2	Azorella selago fjaeldmark	270	very exposed col	2,4	—	—
3	Azorella selago fjaeldmark	145	very exposed ridge	1,6	7,3	1,8
4	Agrostis magellanica mire	130	sheltered valley	0,7	2,6	0,6
5	Azorella selago herbfield	140	sheltered valley	7,6	24,0	6,0

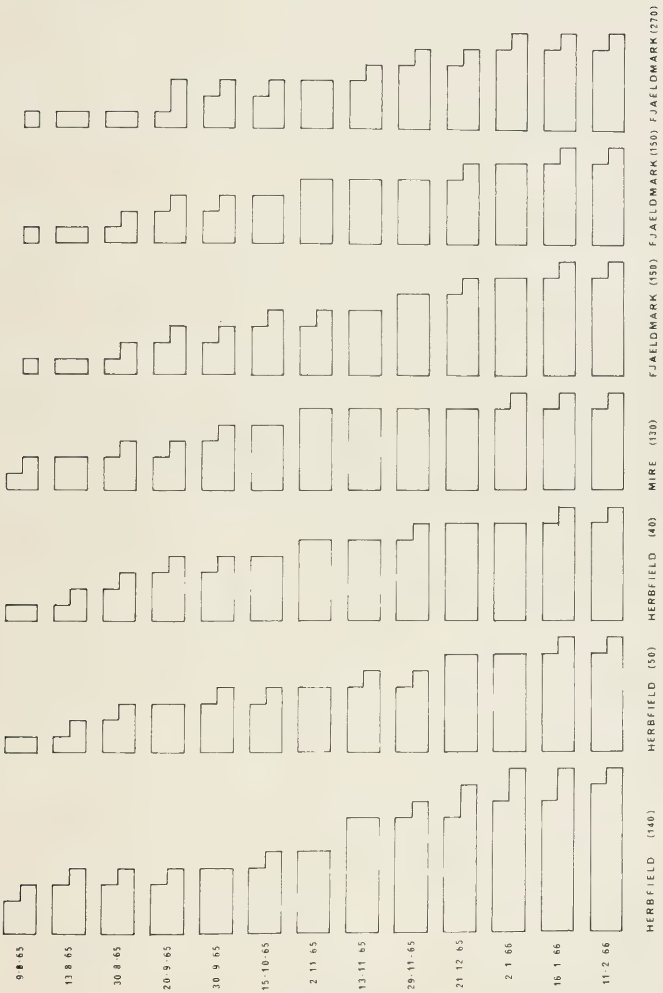

FIG. 4.

Time of appearance of new leaves on branches of *Azorella selago* cushions in populations in herbfield, mire and fjaeldmark communities. Small square represents new bud present, upright rectangle represents new leaf fully opened. The altitude of each population is given in parentheses.

Using the Marion Island data, it is possible to estimate the age of cushions in the various habitats. The height of twenty medium to large cushions in the fjaeldmark populations averaged 15 cm, indicating an age of approximately 83 years for cushions of this size and over a hundred years for the larger cushions. Calculations based on the data for herbfield and swamp communities were of the same order. While it is clear that one cannot assume an even rate of growth throughout a cushion's life history, the data presented above do suggest that one is dealing with extremely slow growing plants, some of which must be of considerable age despite their small size.

Table 3
Shoot production data for three *Azorella selago* cushions collected on Marion Island at the end of the 1969–1970 growth season.

Sample no.	1	2	3
plant community	Herbfield	Fjaeldmark	Fjaeldmark
% cover of A. selago in community	45	10	15
surface area of cushion, sq. m	0,725	0,225	0,095
average no. of shoots per sq. m	24500	38000	42400
average weight per shoot, gms	0,0392	0,0225	0,0211
shoot production, gms per cushion	697	192	85
shoot production, gms/m^2	960	854	895
shoot production, gms/m^2 for community	433	85	134
shoot production, gms/m^2/day for community	1,8[1]	0,4[2]	0,6[2]

1 based on growing season of 255 days
2 based on growing season of 225 days

Primary aerial production. The results of the shoot production measurements are presented in Table 3. These data must be regarded as tentative, pending more detailed studies. The figures do give an indication of the potential productivity of *Azorella selago* however. If it can be assumed that the shoot production in the extensive carpets of *Azorella selago* found in *Azorella selago* Herbfield and *A. selago—Poa cookii* montane herbfield is of the same order as that for the cushions examined in this study, the annual shoot production would be in the region of 960 gms/m^2 or 3,5 gms/m^2/day during the growth season of approximately 255 days. The former figure is approximately six times as high as comparable data for arctic and alpine tundras (Bliss 1966) while the latter figure is within the range of 1 to 4 gm/m^2/day for the same areas (Bliss 1962) which experience a much shorter growing period.

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